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BIOLOGICAL BULLETIN

EXPERIMENTS ON PATTERN-VISION OF THE HONEY BEE.

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Introduction.

In my paper on the "Color Vision of the Honey Bee," published in the BIOLOGICAL BULLETIN for October, 1910, some experiments were described which, I think, demonstrate conclusively that bees can discriminate between colors. In November of that same year, J. H. Lovell¹ published the results of some researches conducted in a manner quite different from my method; but which led him to form the same conclusion.

On page 277 of my paper is the following paragraph: "How minute are the details that bees observe I am not prepared to say; but that they do observe details is indicated by the following observations: (1) In the boxes used in the experiments of Series IV., the trays of the boxes used were entered, from the portice. by means of an eccentric opening. In most of the boxes this doorway was rectangular, in others it was circular. When a bee first approached one of these boxes, she had to search for the entrance. After a few trips she would land on the portico directly in front of the entrance, and, in some cases, she would fly into the tray without even pausing on the portico. (2) For about an hour bees had been collecting honey from some of the red artifacts. It seemed that nearly all of the bees in that part of the field were collecting from those artifacts. Along side of one of the red boxes I placed a red box on the sides and top of which I had pasted bits of white paper. This gave a box with red front and spotted sides. Into this box I placed some honey. The bees that ap-

¹Lovell, J. H., "The Color Sense of the Honey Bee; Can Bees Distinguish Colors," *Amer. Nat.*, Vol. XLIV., Nov., 1910, pp. 673–692.

proached this box from the front always entered immediately; the majority of those that approached the sides paused a moment, then went to the nearest red box." This experiment indicated that bees could discriminate between patterns. The purpose of the researches to be described in this article was the establishment of a definite experimental answer to that question.

The method decided upon was to permit a few bees to learn that honey could be collected easier from artifacts of a certain color pattern than it could be from ordinary flowers; and, after that had been thoroughly learned, to see if those bees could select artifacts of that color-pattern from those of a different color-pattern; 1st, when the artifacts to be selected contained honey and the others did not; 2d, when not only the artifacts to be selected but some of the others also contained honey; 3d, when none of the artifacts contained honey.

The artifacts used were constructed out of cardboard and were of three kinds: circular discs about forty millimeters in diameter,



FIG. 1. A few of the artifacts. From left to right: front view of a transversely striped box, side view of a transversely striped box, front view of a longitudinally striped box, side view of a longitudinally striped box.

cornucopias made in the manner described on page 260 of the article published last year, and special experiment boxes made in the manner described on pages 271 and 272 of that article. The artifacts used this year were smaller than those used last. The cornucopias, excluding the lip, were fifty millimeters long and thirty millimeters in diameter at the largest part. The boxes, excluding the lip, were sixty millimeters long, forty millimeters wide and twenty millimeters high. The pattern that distinguished any artifact was placed upon both the inside and the outside. The following colors and color patterns were used: plain red, plain green, alternate red and green longitudinal stripes, alternate red and green transverse stripes, alternate black and

white longitudinal stipes, mottled red and green. With the exception of the red of some of the plain red artifacts, the red and green used on all of the artifacts was of the same hue. The stripes were about five millimeters wide; the spots on the mottled artifacts varied from two to five millimeters in length; they were irregular in shape and arranged in a haphazard manner.



Fig. 2. A few of the artifacts. From left to right; front view of a mottled box, side view of a mottled box, side view of a longitudinally striped cornucopia, end view of a longitudinally striped cornucopia.

In order to have the bees working under normal field conditions, an abandoned meadow was selected as the site of the experiment plot. Most of the field was rank with *Melilotus alba* Lam.; but here and there were patches of almost barren ground. The majority of the experiments were performed in one of these partly barren spots, in which a few scattered mint plants and a few plants of the white sweet clover were growing.

DESCRIPTION OF THE EXPERIMENTS.

The purpose of this preliminary series of experiments was to permit the bees to learn that honey could be obtained much more easily from artifacts marked with alternate red and green longitudinal lines than it could be from the flowers of the melilot or the mint from which they were foraging.

EXPERIMENT I. Early in the afternoon of July 14, two discs, marked with parallel red and green stripes and well supplied with honey, were attached to the branches of a melilotus bush from which bees were collecting honey.

Although the discs remained on that plant all of the afternoon, no response was made to them by any of the bees.

EXPERIMENT 2. Three discs, marked with parallel red and green stripes, were attached to melilotus twigs and a large drop of

honey placed on each. These were placed in position at eight o'clock on the morning of the fifteenth of July.

These discs were watched until two o'clock in the afternoon; but not a bee made any response to them.

Experiment 3. At about eight A.M., July 17, 1911, two discs, marked with red stripes on a green back-ground were attached to the tops of upright sticks placed in the midst of a mint weed from which several bees were collecting honey. By means of a string the branches of the plant were drawn together in such a manner as to have several blossoms near each of the discs. Honey was placed on the discs and on some of the blossoms near by. Accidentally some honey fell upon some of the leaves.

After waiting, restlessly, in the hot sun, for nearly two hours, I was rewarded for my patience by seeing a bee alight on one of the discs, and, while hanging suspended from its edge, sip the honey. When it had finished and before it started for the hive. the bee made a short flight of orientation. A few minutes later a bee alighted on the top of disc number two and began to sip the honey. Before departing for the hive, it made a flight of orientation. From this time to the close of the experiment, thirty-five visits were made to the discs, twenty to disc one and fifteen to disc two. Often bees were on both discs at the same time. On one occasion, three bees were on disc two and two on disc one. On another occasion, two bees were on each disc. Soon after the bees began to collect from the discs I noticed that several bees were collecting honey that had dropped on the leaves. To check them, wherever I saw honey on a leaf I covered it with dust. By this means I hoped to cause those bees to notice the honey on my artifacts. The habit of collecting from leaves had become fixed and those bees spent the remainder of the afternoon searching the leaves for honey. Occasionally they would find a new supply and collect therefrom until I covered it with dust. By the close of the afternoon, about six bees were collecting from the artifacts and four hunting for honey among the leaves.

EXPERIMENT 4. About two hours before departing for home, disc two was placed in a new position and a cornucopia marked with alternate red and green longitudinal lines was placed where

it had been. Disc one was left in its original position. All of these artifacts were well supplied with honey.

Up to the close of the experiment, eleven visits were made to the artifacts; four to disc number one, three to disc number two, and four to the cornucopia.

EXPERIMENT 5. Half an hour before departing for home, disc number one was placed in a new position and a second cornucopia, resembling number one in its color pattern, was placed in the place rendered vacant by the removal of disc number one. Cornucopia number one and disc number two were left in the positions occupied in experiment 4. All of the artifacts were well supplied with honey.

The bees made twelve visits to these artifacts; four to disc number one, two to disc number two, three to cornucopia number one, and three to cornucopia number two.

Experiment number three was begun at about eight A.M., experiment number five closed at five P.M. Throughout the whole of that interval the artifacts were observed continuously.

On leaving for home all of the artifacts were well supplied with honey and left in the field.

The bees collecting from those artifacts were only a small per cent. of those visiting that part of the field; but they behaved so unlike the others that I could recognize one as soon as it arrived within a yard of the artifacts. The bees that had not begun to collect honey from my artifacts or honey-smeared leaves, on reaching the experimental plot, would simply wander from flower to flower, pausing a moment at some and simply glancing at others. On the other hand, bees that were collecting honey from my artifacts or honey-smeared leaves, on reaching the plot, would describe a number of complex, irregular, number eight curves, no two of which seemed to be in the same plane and which became gradually shorter and shorter until the artifact or honey-smeared leaf was found by the bee. To one looking on, it was almost impossible to resist the belief that those bees were seeking some definite thing or things.

Series II. [July 18, 1911.]

On reaching the field, at about eight thirty A.M., there was no honey in any of the artifacts; but the bees were moving in and

out of the cornucopias as though they were hunting for something.

EXPERIMENT 6. One of the cornucopias used in the last experiment was replaced by an experiment box marked with alternate red and green longitudinal stripes. The other cornucopia was left in place and called striped cornucopia number one. Three groups of three short stakes each were erected near the plant containing the two stakes mentioned above. The groups were about a foot apart and the stakes in each group separated by an interval of about two inches. The groups were numbered from two to four, two being the nearest to the two stakes and four being the most remote. were arranged in a section of a curve. On the top of one of the stakes in each group a cornucopia marked with alternate red and green stripes was placed, while a similar plain red and plain green cornucopia crowned each of the other stakes. In no two groups was the arrangement of the cornucopias the same. In the striped box and in the striped cornucopias, honey was placed. The other artifacts were empty. The position of the artifacts remained the same throughout the experiment.

This experiment began at about nine A.M. and extended until noon. Except during the time consumed in taking a photograph, the artifacts were watched continuously. Not a single visit was made to either the red or the green cornucopias; but forty-seven entrances were made into the cornucopias that were marked with alternate red and green longitudinal stripes. These visits were distributed as follows: striped box number one, nine; striped cornucopia number one, twenty-one; striped cornucopia number two, eight; striped cornucopia number three, seven; striped cornucopia number four, two. Thus all of the striped artifacts were Sometimes a bee would enter one artifact and then leave and enter another and sometimes vet another. It usually sipped honey in the last visited artifact only. In some cases the cause of leaving the first artifact was the presence of some bee; in most cases, however, I could not discover the cause for departing.

EXPERIMENT 7. A fourth group of three stakes was added to the above group and called group five; it was arranged about half way, in a straight line, between group two and group four. All of the

cornucopias were replaced by experiment boxes of the same color patterns. At irregular intervals, the arrangement of the boxes in each group was altered. All of the boxes marked with alternate green and red longitudinal stripes contained honey, the other artifacts were empty.

This experiment extended from noon to five P.M. Except while taking a photograph, the artifacts were watched continuously. During that time not a single entrance was made into either the green or the red boxes; but eighty-nine entrances were made into the striped boxes; and each such box was visited several times. The visits were distributed as follows: striped box number one, eight; striped box number two, fifteen; striped box number three, twelve; striped box number four, seven; striped box number five, twenty-one.

One of the cornucopias used in this experiment leaked and formed, on the slightly inclined stake, a line of honey. Several bees discovered this honey and began to carry it to the hive. The line of honey was on the side of the stake that was turned away from me and I did not know that the bees had formed the habit of collecting honey from the side of the stake until experiment seven was half over. I saw bees flying to that side of the stake; but I supposed they were some of the bees who had formerly formed the habit of collecting honey from smeared leaves, and, since I had seen to it that there was no honey on any of the leaves, I did not give them much attention until I noticed that bees were frequently flying from that place to the hive. As soon as I realized that they had formed that habit, I covered the honev with road dust, hoping to induce the bees to attend to my artifacts. Instead of entering the artifacts, they continued to examine the stake; occasionally one would fly to another stake and examine it. This was not because they had not noticed the artifacts, but because the artifacts had acquired no meaning to them. They would frequently approach one of the boxes containing honey and hover before it momentarily and then return to searching the stakes. To them the stakes had come to mean "honey-bearers" and they seemed to use the artifacts and neighboring plants as reference points.

Most of the bees continued to describe those complicated num-

ber eight curves, whenever they arrived at the experiment plot; but the number of curves described were perceptibly fewer and the lengths much shorter, and some of the bees seemed to fly practically direct to the artifacts.

On departing for home, all of the artifacts, except three striped boxes, were removed. Those boxes were well supplied with honey.

July nineteenth, I arrived at the field at 9:30 A.M. and found the boxes empty and the bees flying into and out of them as though hunting for something. It began to rain soon after my arrival, which made it impossible to continue my experiments that day. On leaving, all of the artifacts were removed from the field.

The morning was quite cloudy and when I arrived in the field, at about half past seven, the bees were not foraging.

Experiment 8. Three groups of three experiment boxes each were arranged in the manner described above. In each group there was one box marked with alternate red and green longitudinal stripes, one green box and one red box. The order of the boxes was different in each group. When the experiment was about half over, the arrangement of the boxes in each group was changed. All of the boxes marked with alternate red and green longitudinal stripes contained honey; the others were empty. The experiment was an hour long.

Twenty-five entrances were made into the interior of the striped boxes; but not a single entrance into either the red or the green boxes. The visits were distributed as follows: striped box number one, ten; striped box number two, eight; striped box number three, seven. Only once did a bee, on arriving at the plot, make the irregular number eight curves mentioned above. On arriving at the plot, the bee would either fly directly to one of the striped boxes, or else fly along, examining box after box, until it reached a striped box. On leaving, the bees did not always make flights of orientation. Often a bee would arrive at the hind end of one of the experiment boxes that contained honey and attempt to find an entrance; then it would sidle around to the front end and enter.

EXPERIMENT 9. Three groups of boxes were arranged as in

experiment eight; but honey was placed, not only in the striped box, but also in red box number one and green box number two. When the experiment was about half over, red box number one was placed where striped box number one had been and striped box number one placed on the stake made vacant by the removal of red box number one; and green box number two was placed where striped box number two had been and that striped box placed on the stake made vacant by the removal of green box number two. The time occupied was about one hour.

Twenty-two entrances were made into the striped boxes, half before and half after the change was made in the arrangement of the boxes; but not a single visit was made into the interior of either the red or the green boxes, although one box of each of those colors contained honey. The visits were distributed as follows: striped box number one, thirteen; striped box number two, four; striped box number three, five. One bee hovered before the hind end of red box number one for several seconds and then flew to striped box number one. Another bee alighted on the front end of red box number one and then departed. Bees often paused momentarily before all of the boxes; but they never entered any that were not marked with alternate red and green longitudinal stripes.

Experiment 10. Three groups of boxes were arranged as in experiment eight; but no honey was placed in any of the boxes and none had ever contained honey. The duration of the experiment was about fifteen minutes.

Fourteen entrances were made into the striped boxes; but not a single visit was made to the interior of either the green or the red boxes. The visits were distributed as follows: striped box number one, six; striped box number two, three; striped box number three, four.

EXPERIMENT II. Two groups of artifacts were removed from the field; thus leaving only one group of boxes, all of which were empty and none of which had ever contained honey. The time allowed was about ten minutes.

Ten entrances were made into the striped box, but not a single visit was made to the interior of either of the other boxes. When I terminated the experiment, about six bees were hovering about the striped box, examining it carefully.

Series IV. [July 21, 1911.]

EXPERIMENT 12. Two sets of five boxes were arranged on stakes. In each group there was one of each of the following artifacts: box marked with alternate red and green longitudinal stripes, box marked with alternate black and white longitudinal stripes, box mottled with green and red, a plain red box, and a plain green box. The arrangement of the boxes in each group was different, and was changed twice during the experiment. The box marked with alternate red and green longitudinal stripes was supplied with honey; the others were empty. The time consumed was about one and a half hours.

Sixty-three entrances were made into the boxes marked with alternate red and green longitudinal stripes and one into the boxed mottled with green and red; no visits were made into the interiors of any of the other boxes. Bees frequently hovered before other boxes and twice bees alighted on the portico of the box marked with alternate black and white longitudinal stripes, but did not enter. The visits to the artifacts marked with alternate red and green longitudinal stripes were distributed forty-two to box one and twenty-one to box two.

Experiment 13. One set of six boxes was arranged on stakes. To the kinds of boxes used in experiment 12, I added a box marked with alternate red and green longitudinal stripes. The box marked with longitudinal red and green stripes was supplied with honey; the others were empty. Starting at the left, the arrangement of the boxes was as follows: plain green, marked with alternate red and green longitudinal stripes, mottled with green and red, marked with alternate black and white longitudinal stripes, plain red, marked with alternate red and green transverse stripes. The time consumed was about half an hour.

Nineteen entrances were made into the box marked with alternate red and green longitudinal stripes; but no visits were made to the interior of any other box.

EXPERIMENT 14. The same number and kinds of boxes were used as in experiment thirteen; but the mottled red and green box was placed where the box containing honey had been and the box containing the honey was placed on the stake rendered vacant by the removal of the mottled box. The time consumed was about half an hour.

Twenty entrances were made into the box marked with alternate red and green longitudinal stripes and one into the box that was mottled with red and green. No visits were made into the interior of any other box.

EXPERIMENT 15. The same number and kinds of boxes were used as in experiment fourteen; but the box marked with alternate red and green transverse stripes was placed where the box containing the honey had been, and the box containing the honey was placed where the box marked with alternate red and green transverse stripes had been. The time consumed was about three-quarters of an hour.

Thirty-six entrances were made into the box marked with alternate red and green longitudinal stripes, six into the box marked with alternate red and green transverse stripes, and two into the box marked with alternate black and white longitudinal stripes. No visits were made into the interior of any other box. The bees that selected the wrong boxes did not enter them as promptly as did those that entered the right box. In each case the bee hovered before the entrance quite a while before entering. All of these mistakes were made during the first ten minutes of the experiment.

EXPERIMENT 16. Two boxes marked with alternate red and green longitudinal stripes and two boxes marked with alternate red and green transverse stripes were arranged on stakes, in a line, with all of the entrances facing in the same direction. For the first half of the experiment the different kinds of boxes alternated; during the latter half, the boxes with the longitudinal stripes were in the middle. The boxes with longitudinal stripes contained honey, the others were empty. The time consumed was about half an hour.

The purpose of this experiment was to accustom the bees to ignoring the transversely striped boxes. Thirty-three entrances were made into the longitudinally striped boxes and none into any of the others.

EXPERIMENT 17. The same number and kinds of boxes were used as in experiment fifteen and they were arranged in the following order: box marked with alternate black and white longitudinal stripes, box marked with alternate red and green transverse stripes, box marked with alternate red and green longitudinal stripes, plain green box, box mottled with red and green. The box marked with

longitudinal red and green stripes contained honey; the others were empty. The time consumed was about fifteen minutes.

Eleven entrances were made into the box marked with alternate red and green longitudinal lines; no entrances were made into any of the other boxes.

EXPERIMENT 18. The same kind and number of boxes were used as in the above experiment, but they were arranged in the following order: box marked with alternate black and white longitudinal stripes, box marked with alternate red and green transverse stripes, plain green box, box marked with alternate red and green longitudinal stripes, box mottled with red and green, plain red box. None of the boxes contained honey or ever had contained honey. The time consumed was about fifteen minutes.

Thirty entrances were made into the box marked with alternate red and green longitudinal stripes, but no visits were made into the interior of any other box.

Experiment 19. An empty box marked with alternate red and green longitudinal stripes and which never had contained honey was placed on the palm of my hand and by its side was placed an empty box marked with one of the other patterns. The entrances of both boxes were made to face the same way. All other artifacts were removed from the field and my hand held near the stakes upon which artifacts had rested. At the end of about two minutes the position of the boxes was altered. This maneuver was repeated with each kind of box used in experiment eighteen.

At least a hundred entrances were made into the box marked with red and green longitudinal stripes; but not a bee entered any of the other boxes. One bee acted as though it was going to enter the box marked with alternate red and green transverse stripes, but it did not do so. Towards the end of the experiment the bees entered the box marked with alternate red and green longitudinal stripes so rapidly that it was almost impossible to keep an accurate record. To one looking on, it seemed as though the bees were looking for something which they expected to find in those boxes.

When I left for home the bees were searching over and around the barren stakes for something that was not.

INTERPRETATION OF THE EXPERIMENTS.

These experiments furnish additional evidence, if such is needed, that Plateau is mistaken when he claims that odor is the sole factor that leads bees to the honey of flowers; for my discs, marked with red and green stripes and well supplied with honey, remained exposed to bees for fully two days before a single bee collected honey from them [Ex. 1–5].

These experiments strengthen the impression, gained from previous work with hymenopterous insects, that such insects can be induced to form new associations that will influence their behavior, if only the experiment is so planned as to lead the insect to accidentally make the association. So far as my experience goes, it is almost impossible to coerce them into forming new associations, and an abundance of time is often required for the formation of chance associations. Lack of response to a stimulus does not mean that that stimulus has not been noticed by the insects; but that, to them, it has not yet acquired a meaning.

In inducing bees, in the field, to respond to new food-objects, the new associations are formed much more quickly when the food is exposed to view than when it is hidden. They may be induced to form such associations, however, even under the latter conditions. These statements are supported by the fact that last year, when I conducted a lengthy series of experiments with discs and cornucopias, artifacts which did not hide the honey from view, I soon had more bees responding to the artifacts than I could keep an accurate record of; whereas this year, when I laid aside my discs and cornucopias as soon as about half a dozen bees had made the association, at no time were more bees at work than could be counted. At the close of the series about twice as many bees were collecting from the artifacts as at the beginning.

When a bee had discovered one of my honey-producing artifacts and collected therefrom, it would make a flight of orientation and then fly home. On returning to the field it would, by means of a series of ever narrowing, complex, figure eight curves, search out the experiment plot, and then, by a closer scrutiny of the surrounding objects, locate the artifact desired. [Last

paragraph of Series I.] After a bee had made several trips to the plot, it would fly directly to it without making the complicated searching movements. This striking behavior furnished a sure means of telling when a new bee had formed the association. I changed the arrangement of the individual artifacts so often that the bees usually were forced to search for the honey-producing box. After the association had been well established, the bees usually departed for home without making a careful flight of orientation. If, however, I had made a marked change in the position of the artifact since the last visit of the bee, then a careful flight of orientation was always made. No one who had watched these pronounced searching movements could doubt that bees are largely guided by memory pictures of the environment.

After a bee had learned, by experience, that artifacts bearing a certain color pattern contained a more copious supply of easily obtained honey than ordinary flowers, it would select artifacts bearing that color pattern from those marked in a different way. This was true: (1) when several of the artifacts to be selected were scattered among a number of plain artifacts of the colors used in making the color-pattern [Ex. 6-11]; (2) when the artifact to be selected was scattered among several other artifacts, some of which were plain and some of which were marked with patterns unlike that of the artifact to be chosen [Ex. 12-15, 17, 18]; (3) when the only difference between the artifacts was that one was marked with transverse and the other with longitudinal stripes [Ex. 16]; (4) when the artifact to be selected contained the honey and the others did not [Ex. 8, 12-17]; (5) when honey was to be found not only in the artifact to be selected, but in some of the other artifacts also [Ex. 9]; (6) when none of the artifacts contained honey [Ex. 10, 11, 18, 19].

All of the facts mentioned in the above paragraph are recorded in the following table.

Although this table shows conclusively that bees can recognize color patterns it does not tell the whole story. It does not show that two of the mistakes were made in selecting a box mottled with red and green for one marked with longitudinal red and green stripes; that two mistakes consisted in selecting a box marked with black and white longitudinal stripes for one marked with

TABULATED RESPONSES OF HONEY BEES TOWARDS PATTERNS.

The bee to select an artifact marked with alternate red and green longitudinal stripes when associated with	No. of Trials.	No. of Successes.	No. of Failures.	Per Cent. of Successes.
Plain red and plain green artifacts, an equal number of the three kinds being used; when the artifact to be selected contained honey and the others did not	161	161	0	100.0
and some of each of the other kinds contained honey	22	22	0	100.0
Plain red and plain green artifacts, an equal number of each of the three kinds; none of the artifacts contained honey Artifacts marked with alternate red and green transverse	24	24	o	100.0
stripes; the artifacts to be selected contained honey, the others were empty	33	33	0	100.0
one of each of the following artifacts: plain green, plain red, mottled red and green, marked with alternate black and white longitudinal stripes, marked with alternate red and green transverse stripes; the artifact to be selected con-	64	63	1	98.5
tained honey, the others were empty One of each of the following artifacts: plain green, plain red, mottled red and green, marked with alternate black and white longitudinal stripes, marked with alternate red and		75	9	89.3
green transverse stripes; none of the artifacts contained honey	30	30	0	100.0
contained honey	100	100	1	100.0
Grand total	1518	508	10	98.5

red and green longitudinal stripes, and that the other six mistakes consisted in selecting a box marked with red and green transverse stripes for one marked with red and green longitudinal stripes. And it does not show that the bees soon learned to avoid making even these mistakes.

There was much in the behavior of these bees to indicate that, in their ability to distinguish minute details, they are near sighted. On examining the artifacts, either when searching for an artifact or in making its flight of orientation, the bee always hovered within about a centimeter of the object examined. The first box a bee reached, on arriving at the plot, was usually not the desired one, and, after a momentary examination, it would pass on to the next.

Evidently bees can distinguish between color-patterns, and this is of value to them in recognizing plants that yield honey. Hence, since insects can distinguish colors and the fine details of color pattern, there is nothing about the visual powers of bees that militates against the theory that the colors and the color markings of flowers are adaptations to insect visitors.

SUMMER HIGH SCHOOL, St. Louis, Mo., July 22, 1 11.